# *LEPTOPTERYGIUS TENUIROSTRIS* AND OTHER LONG-SNOUTED ICHTHYOSAURS FROM THE ENGLISH LOWER LIAS

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ABSTRACT. One of the commonest ichthyosaurs from the English Lower Lias is the long-snouted species *Leptopterygius tenuirostris*, known principally from Street, Somerset. Because of the vagaries of preservation there are few complete skeletons, and the problem is exacerbated by the occurrence of composite specimens. The authenticity of a quarter of the specimens studied here is in doubt, and hence caution is needed when working on material from Somerset. The occurrence of a tail bend in *L. tenuirostris* is confirmed by the presence of wedge-shaped centra in the caudal region of several skeletons. The vertebral column was probably not steeply downturned, and may have been essentially straight in life.

*Eurhinosaurus*, unusual for its abbreviated mandible, may be closely related to *L. tenuirostris* and is therefore of interest here. The suggestion that it occurs in the Upper Lias of England is confirmed. The contention that *Eurhinosaurus* lacked a tail bend is questioned because a wedge-shaped centrum has been identified in one specimen.

Two trivial names besides *tenuirostris* have been used for long-snouted ichthyosaurs: *latifrons* and *longirostris*. The former is a *taxon dubium*, while the latter should be used only in combination with *Eurhinosaurus*.

ICHTHYOSAURS occur throughout most of the Mesozoic, but they are best known from the Lower Jurassic, where large numbers of complete or near-complete skeletons have been found, sometimes in remarkably good states of preservation. Especially prolific have been the Lower Lias (Hettangian, Sinemurian, and Lower Pliensbachian) outcrops of south-west England, and the Upper Lias (Toarcian) deposits of southern Germany. Upper Lias ichthyosaurs occur in England, notably in the Whitby area of Yorkshire, and in the vicinity of Ilminster, Somerset, but neither locality has been very productive, and the Whitby material is generally not well preserved. The temporal separation between the Upper and Lower Lias is about 15 million years (Harland *et al.* 1982) and, although the two faunas have similar diversities of forms, they are taxonomically distinct. Both faunas, for example, have a short-snouted form; *Ichthyosaurus breviceps* in the Lower Lias and *Stenopterygius hauffianus* in the Upper Lias. While the present paper is primarily concerned with Lower Lias ichthyosaurs, some taxonomic problems require reference to Upper Lias material.

The commonest English species, accounting for about half of the determinate skeletons, is *I. communis*, a moderately sized ichthyosaur reaching a maximum total length (measured from the tip of the snout to the tip of the tail) of about 2·5 m (McGowan 1974*b*). Less common in terms of complete skeletons, but abundantly represented by isolated humeri, partial fins and rostral segments, is *Leptopterygius tenuirostris*, characterized by its relatively long slender rostrum. *L. tenuirostris* is somewhat larger than *I. communis*, reaching lengths in excess of 2·5 m. While it has been found at several Lower Lias localities, it is best known from Street and the surrounding areas of Somerset. Because of the vagaries of preservation, *L. tenuirostris* is not so well known as *I. communis*, and one uncertain point is whether there was a tail bend. The tail bend, a prominent feature of post-Triassic ichthyosaurs, marks the position of the caudal peduncle, where the vertebral column is downturned to support the hypocaudal lobe of the tail (McGowan 1974*a*). The most completely preserved skeletons (BGS 51236 and BMNH R498—see McGowan 1974*b*, figs. 11 and 12*a*) appear to lack a tail bend, raising the question of whether an asymmetrical caudal fin was

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present in this species. Absence of a reversed heterocercal tail, however, may not be unique among ichthyosaurs because it has recently been proposed that *Eurhinosaurus*, an Upper Lias genus bearing a superficial resemblance to the modern swordfish, lacked this feature (Riess 1986). This is of particular interest here because of the possibility that *L. tenuirostris* lies close to the ancestry of *Eurhinosaurus* (McGowan 1986).

While most long-snouted ichthyosaurs from the Lower Lias have been referred to *L. tenuirostris*, two other names, *I. longirostris* and *I. latifrons*, have also been used, sometimes synonymously and frequently causing much confusion. An additional problem is caused by incomplete preservation, especially of the narrow tip of the snout and mandible, and also by changes that have been made to specimens during preparation. Some of these modifications are easily recognized, but others have been so skilfully executed that their detection is difficult, even when it is possible to dismantle the entire skeleton (McGowan *et al.*, in prep.). It is, therefore, necessary to be especially circumspect when dealing with material from Somerset localities.

In a previous description of *L. tenuirostris* (McGowan 1974*b*) attention was drawn to the problem of assigning the species to an appropriate genus. The decision was taken to refer it to *Ichthyosaurus* but, in the light of new information presented here, this is no longer appropriate. The species is accordingly referred to *Leptopterygius*, a genus erected by Huene (1922) for *L. tenuirostris*, and several other species. This usage is consistent with that of Appleby (1979), but I do not use his ordinal designations, which are based upon the recognition of latipinnate and longipinnate ichthyosaurs. These latter terms are based on fin structure, and they have been widely used for classification. I once considered that there were also correlated cranial characters which could be used to distinguish between the two groups (McGowan 1972), but I later questioned the validity of the dichotomy (McGowan 1976), and concluded that there were no unequivocal distinctions between latipinnate and longipinnate ichthyosaurs (McGowan 1979, pp. 125–126). Huene (1922) did not give a diagnosis for *Leptopterygius* and Appleby (1979, p. 943), considering it to be a monotypic genus, gave the same diagnosis as for the species *L. tenuirostris*. Although a redefinition of *Leptopterygius* is clearly needed, this requires a review of several other species and therefore lies beyond the scope of the present work.

There are three primary objectives of this paper: to clarify the taxonomy of *I. longirostris* and *I. latifrons*; to assess the available long-snouted specimens, assigning them to their appropriate taxa and assessing their authenticity where this is in doubt; and, to use these additional data to revise the previous description of *L. tenuirostris* (McGowan 1974*b*). Secondary objectives are to examine the question of whether *Eurhinosaurus* occurs in the English Upper Lias, and to make some preliminary remarks on the tail of this genus. The reason for including *Eurhinosaurus* here is partly because of the taxonomic confusion which has existed between this long-snouted form and *L. tenuirostris*, and also because of the possible phylogenetic relationship between them (McGowan 1986).

## MATERIALS AND METHODS

Of the specimens examined from England, twenty-seven are from the Lower Lias (primarily from Street, Somerset) and two from the Upper Lias of Whitby. Reference is also made to three specimens of *Eurhinosaurus* from the Upper Lias of Germany. Abbreviations used are: BATGM, Bath Geological Museum (the ichthyosaur material, which is part of the Moore Collection, has been on loan to the National Museum of Wales, Cardiff, for the last several years); BGS, British Geological Survey, Keyworth, Nottinghamshire (the ichthyosaur BGS 51236 is currently in the Geological Museum, London); BMB, Admiral Blake Museum, Bridgwater, Somerset; BMNH, British Museum (Natural History), London; DLR, Dinosaurland, Lyme Regis, Dorset; FSF Forschungsinstitut Senckenberg, Frankfurt (Natur-Museum, Senckenberg), Germany; GTS, Alfred Gillett Trust, Street, Somerset (this collection is located in the archives of C and J Clark Ltd.); LEICS, Leicestershire Museums, Art Galleries and Records Service, Leicester; OUM, Geological Collections, University Museum, Oxford; SCM, Somerset County Museum, Taunton; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; WM, Wells Museum, Somerset. Specimens lacking catalogue numbers are referred to by MS numbers, given in quotation marks.

Body lengths were measured along the vertebral column using a steel tape and recorded to the nearest millimetre. The same tape was used for all measurements in excess of 550 mm. Small dial calipers and large vernier calipers were used for measurements less than 550 mm, recorded to the nearest 0·1 and to the nearest 1 mm, respectively. Details of the characters measured and the ratios derived from them are given elsewhere (McGowan 1974*a*; 1976) and are summarized in Table 1.

TABLE 1. Characters recorded and ratios derived.

| | |
|---|---|
| | AXIAL SKELETON |
| Vertebral count to pelvis | Number of vertebrae from atlas to level of pelvis. |
| Vertebral count to tail bend | Number of vertebrae from atlas to level of tail bend. |
| Total vertebral count | Number of vertebrae from atlas to end of column. |
| Presacral length | Length from atlas to level of pelvis, measured along vertebral column. |
| Preflexural length | Length from atlas to level of tail bend, measured along vertebral column. |
| | FINS AND GIRDLES |
| Number of primary digits | Number of digits arising from carpus. |
| Total digital count | Sum of primary and secondary (arising from outside carpus) digits |
| Elements in longest digit | Number of elements in longest digit, counting from epipodials. |
| Humerus length | Maximum length, measured between horizontals perpendicular to shaft. |
| Humerus width | Maximum distal width, measured between verticals parallel to shaft. |
| Humerus shaft | Minimum width of shaft. |
| Femoral length | Maximum length, measured between horizontals perpendicular to shaft. |
| Femoral width | Maximum distal width, measured between verticals parallel to shaft. |
| Pelvic condition | Pelvis tripartite (pubis and ischium unfused), or bipartite (fused). |
| Coracoid length | Maximum anteroposterior length. |
| Coracoid width | Maximum lateromedial width. |
| Coracoid notching | Anterior and/or posterior margins emarginated. |
| | SKULL |
| Skull length | Distance between tip of snout and posterior edge of quadrate. |
| Jaw length | Distance between tip of dentary and posterior edge of angular. |
| Orbital diameter | Internal diameter of orbit, measured along its longitudinal axis. |
| Snout length | Distance between tip of snout and anterior (internal) margin of orbit. |
| Premaxillary length | Distance between tip of snout and anterior tip of maxilla. |
| Prenarial length | Distance between tip of snout and anterior margin of external naris. |
| Sclerotic diameter | Internal diameter of sclerotic ring measured along its longitudinal axis. |
| Overbite | Distance between tip of snout and tip of jaw. |
| Orbital ratio | Orbital diameter divided by jaw length. |
| Snout ratio | Snout length divided by jaw length. |
| Premaxillary ratio | Premaxillary length divided by jaw length. |
| Prenarial ratio | Prenarial length divided by jaw length. |
| Sclerotic ratio | Sclerotic diameter divided by orbital diameter. |

In addition, several measurements have been found useful for comparing the relative slenderness of skulls and jaws. These measurements are obviously sensitive to compression distortion and, since there is no way of assessing how this might vary from one specimen to another, the measurements are used only for comparative purposes and do not contribute to the diagnosis of *L. tenuirostris*.

1. Snout depth at the tip of the maxilla (abbreviated S-M)—the minimum depth of the snout, measured at right angles to the longitudinal axis of the skull, at the level of the anterior tip of the maxilla.
2. Snout depth at the naris (S-N)—the minimal depth of the snout, measured at right angles to the longitudinal axis of the skull, at the level of the anterior end of the external naris.
3. Snout depth at the mid-point of the snout (S-S2)—the minimal depth of the snout, measured at right angles to the longitudinal axis of the skull, at a point one-half of the snout length back from its tip.

4. Snout depth at the mid-point of the jaw (S-J2)—the minimal depth of the snout, measured at right angles to the longitudinal axis of the skull, at a point one-half of the jaw length back from its tip.

5. Jaw depth at the tip of the maxilla (J-M)—the minimal depth of the jaw, measured at right angles to the longitudinal axis of the jaw, at the level of the anterior tip of the maxilla.

6. Jaw depth at the naris (J-N)—the minimal depth of the jaw, measured at right angles to the longitudinal axis of the jaw, at the level of the anterior end of the external naris.

7. Jaw depth at the mid-point of the snout (J-S2)—the minimal depth of the jaw, measured at right angles to the longitudinal axis of the jaw, at a point one-half of the snout length back from its tip.

8. Jaw depth at the mid-point of the jaw (J-J2)—the minimal depth of the jaw, measured at right angles to the longitudinal axis of the jaw, at a point one-half of the jaw length back from its tip.

The tail bend is usually an obvious feature in skeletons with complete or near-complete vertebral columns and its identification is therefore usually a simple matter. However, care has to be taken to ensure that a given tail bend is natural and not an artefact of preparation. This is because a tail bend can be manufactured, unwittingly or otherwise, simply by inclining a block containing the terminal portion of the vertebral column to the rest, and I suspect that several ichthyosaur skeletons have been so modified. The position of the tail bend in specimens lacking an obvious flexion can be estimated by detecting the changes in diameter of the centra in its vicinity (McGowan 1974*a*, pp. 4–6). However, the only way to establish unequivocally the position of the tail bend is to identify the three or so wedge-shaped centra that form its apex (McGowan 1974*a*, fig. 3*b*). Since the distinctive shape of these apical vertebrae can only be seen when they are exposed in lateral view, which is seldom the case, confirmation is usually not possible.

## TAXONOMIC STATUS OF *I. LONGIROSTRIS* AND *I. LATIFRONS*

### I. longirostris

Although this species is usually attributed to Owen 1881 the first description, albeit brief, was given by Mantell (1851, p. 385) based upon a badly crushed skeleton from Whitby, Yorkshire, said to be remarkable for its exceedingly slender and elongated snout. Lydekker (1889, p. 91) identified Mantell's specimen as BMNH 14566, noting that it was from the Upper Lias, and that it had been figured by Owen (1881, pl. 32, fig. 8). BMNH 14566 is therefore the holotype of *I. longirostris* Mantell 1851.

Jäger (1856), dissatisfied with Mantell's brief description, gave one of his own which included some additional material, namely an almost complete but distorted skull from the Upper Lias of Germany (SMNS '438'). He noted that the mandible of this specimen seemed foreshortened, but that this was apparent rather than real and that the mandible did extend to the tip of the snout. After examination of the material, I concluded that the mandible really was shortened, and that this specimen should therefore be referred to the genus *Eurhinosaurus* (McGowan 1979, p. 131). Indeed, most authors, including Huene (1922) and Kuhn (1934), give the authority of the species *E. longirostris* as Jäger (1856). However, the authority for the name *longirostris* is Mantell 1851, erected upon BMNH 14566, and it is now necessary to determine whether this material, like Jäger's (1856) additional material, is referable to *Eurhinosaurus*.

Huene (1922, p. 39) noted that the skull of BMNH 14566 was exposed from the dorsal aspect and the mandible was not visible, but he surmised that it was shortened because he believed that the material appeared to belong to *Eurhinosaurus*. I have now had the opportunity of examining this rather incomplete specimen, and agree with Huene's conclusions (see p. 416). Thus BMNH 14566 appears to be referable to *Eurhinosaurus*, and is therefore regarded as the holotype of *E. longirostris* (Mantell 1851).

Owen's (1881) description of *I. longirostris* was founded upon material from the Lower Lias of Barrow-on-Soar, primarily upon BMNH 36182 which may be regarded as his holotype. But the name *I. longirostris* was already occupied by Mantell's (1851) species, which belongs to a different genus (*Eurhinosaurus*). Owen somewhat confused the issue further by including a figure of the skull of BMNH 14566 in his description of *I. longirostris*, but, since he did not discuss this material, and since his species was primarily erected upon BMNH 36182, the name *I. longirostris* Owen 1881 may be regarded as a junior primary homonym and accordingly rejected.

I. latifrons

Owen (1881, p. 119) correctly attributed this species to König (1825, pl. 19, fig. 250) who had figured a partial skull and incomplete vertebral column from the Lower Lias of Barrow-on-Soar. This specimen was subsequently identified by Lydekker (1889, p. 90) as BMNH R1122. Owen (1881, pl. 27, fig. 1) gave a detailed figure of the skull, and (p. 119) referred a second specimen to the species, 'a skeleton, lacking both ends, but including the trunk, with chief part of the skull . . . the total length being 4 feet 10 inches'. He gave the locality as Lyme Regis (and also for König's material), but Lydekker (1889, pp. 90–91), who identified this second specimen as BMNH 38709, gave the locality as Barrow-on-Soar. I do not consider either specimen to be adequate for the erection of a species, and therefore reject the name *I. latifrons* König 1825 as a *taxon dubium*, *sensu* Smith (1970).

## SYSTEMATIC PALAEONTOLOGY

Identifying specimens that have been modified during preparation proved to be a major problem during this study. Almost a quarter of the specimens show evidence of having been modified, and some of these are obvious composites. Others are less readily detected, and it is largely due to this uncertainty that the descriptive account of *L. tenuirostris* is tempered with a degree of caution.

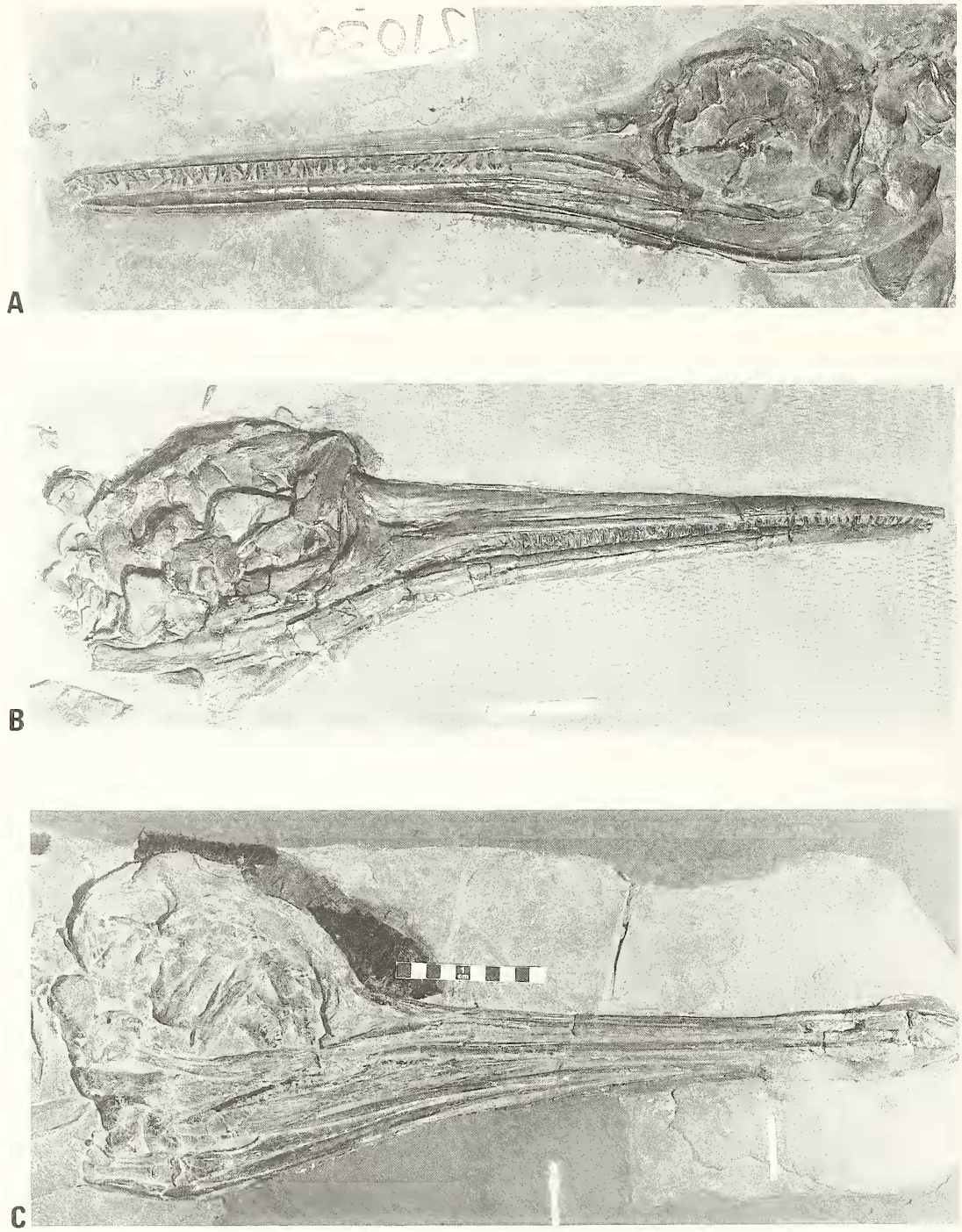
Seven of the twenty-nine specimens studied will not be treated further here as they have almost certainly been modified during preparation (BMB C2, BATGM M3560, BATGM M3558, BATGM M3568, BATGM M3575, OUM 10319, BATGM M3564). Four more specimens are too incompletely preserved to be identified (BMNH R1123, BMNH 38709, BATGM M3573, GTS L/AG/Arch/7), and a fifth (BMNH R1120), which may also be largely indeterminate, was inaccessible because of building construction. A large and fairly complete skeleton (DLR '001'), which is probably not referable to *L. tenuirostris*, may represent a new species. Treatment of this specimen, however, will be postponed until some comparable material, recently acquired by the City of Bristol Museum and Art Gallery, has been studied.

Twelve of the remaining specimens are referred to *L. tenuirostris*, mostly without qualification (OUM J10305, BMNH R489, BGS 51236, SCM 8372, WM 527, GTS L/AG/Arch/18, BATGM M3552, BATGM M3556, BATGM M3565, BATGM M3566, LEICS OS.90.1953, DLR '002'). Two more specimens (BMNH 2009 and BMNH 36182) probably represent variant individuals of the species. Two specimens, BMNH 14566 and BMNH 36876, are referred to *E. longirostris*, confirming the occurrence of this genus in the Upper Lias of England.

L. tenuirostris (Text-figs. 1 and 2)

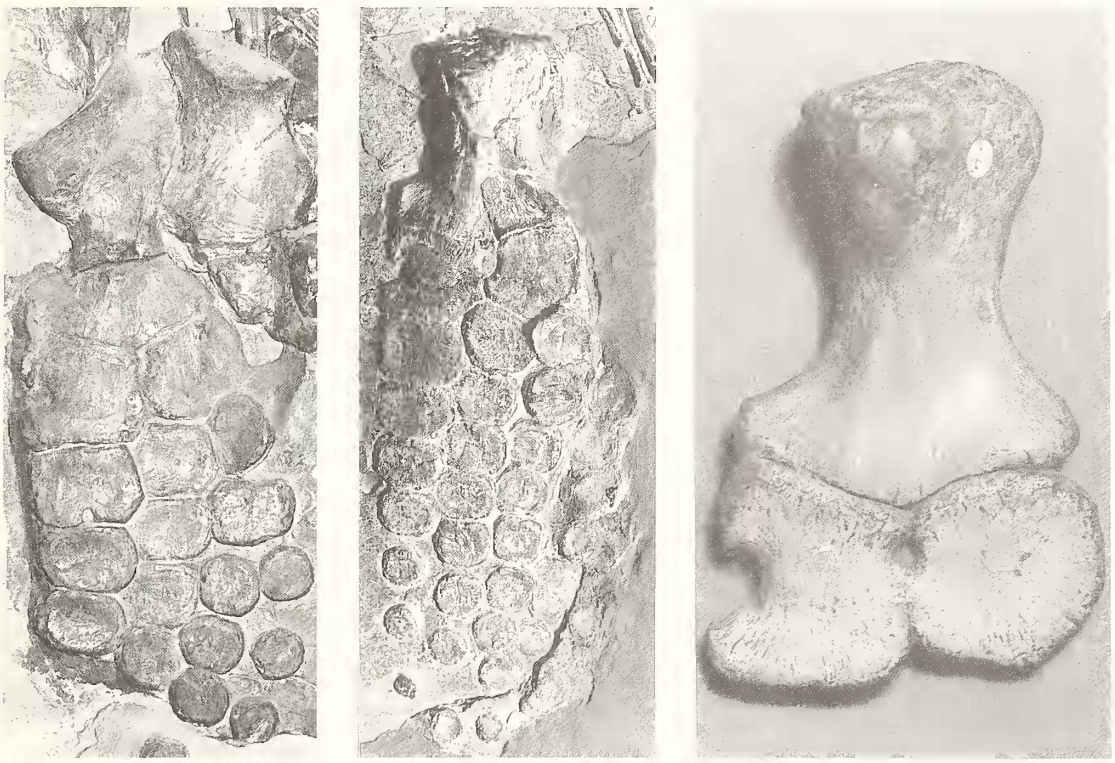
The picture that emerges of *L. tenuirostris* is that of a long-snouted, long-bodied ichthyosaur with a tail bend which is probably not steeply downturned and which may in life have been essentially straight. The vertebral counts to the pelvis and to the tail bend are in the region of 45 and 85 respectively. The forefin has four major digits, each with relatively few phalanges, and the number of elements in the longest digit is only about 15. The phalanges are large, discoidal, and probably well spaced distally. The humerus has a constricted shaft, broadly expanded distally, with a facet on its leading edge. The radius has a deep notch on its leading edge and frequently encloses a small foramen along its contact edge with the ulna. Fusion sometimes occurs between the radius and ulna and between the radius and the humerus (Table 2). The forefin is so distinctive that it is possible to identify isolated fins, even partial ones. However, since similar forefin features are also found among Upper Lias ichthyosaurs, such identifications can only be made if the material is known to be from the Lower Lias.

The pelvic girdle is tripartite, with distinct and separate ilium, ischium, and pubis. Fusion sometimes occurs between the pubis and the ischium, but this is only partial and does not give rise to the essentially single ischio-pubic element as found in the Upper Lias genus *Stenopterygius* (McGowan 1979). The coracoid is rounded and, while an anterior notch, often small and discrete, always appears to be present, there is usually not a posterior one. The coracoid seen in BGS 51236 has an unusual rectilinear shape and might not be natural.




TEXT-FIG. 1. *Leptopterygius tenuirostris*. A, OUM J10305, ×0·23; B, BGS 51236, ×0·22; C, SCM 8372, ×0·22.

The architecture of the skull is dominated by the extremely long slender snout and the equally slender mandible. The orbit, which often approaches a perfect circle, dominates the post-rostral segment of the skull but, relative to the length of the skull, it is fairly small. The orbital ratio is therefore relatively low, usually lower than that of the commonest Lower Lias species, *I. communis*. The external naris, rather than being a simple opening, is more often a bilobed structure which is sometimes quite complex. In some instances it appears to be drawn out anteriorly into a narrow slit, but this might be a result of preservation. The teeth are slender rather than conical and there is a tendency towards tooth reduction, both in their size and number, with increasing maturity. A similar situation occurs in the common Upper Lias species *S. quadriscissus* (Huene 1922, p. 40; McGowan 1979, pp. 102–104). A variation seen in some specimens is for the tip of the snout to extend beyond that of the mandible, giving the skull an overbite. There is a possible overbite of 9 mm in OUM J10305, a definite one of 19 mm in BGS 51236, and an overbite of between 60 and 70 mm in BMNH 2009, which is about 15% of the snout length.




TEXT-FIG. 2. *Leptopterygius tenuirostris*. A, OUM J10305, ×0·32; B, SCM 8372, ×0·32; C, BMNH R1127, an isolated partial fin, ×0·62. For ease of comparison, photographs B and C have been laterally inverted; all three appear to be left fins in dorsal view.

*Emended diagnosis*. Vertebral count to tail bend (which may be indistinct) > 79; vertebral count to pelvis at least 44 but probably not exceeding 50; orbital ratio < 0·25 and may be < 0·20; snout ratio > 0·70; premaxillary ratio > 0·48; prenarial ratio > 0·56; sclerotic ratio ⩾ 0·34; teeth predominantly slender and may be relatively small; forefin probably with four digits; humerus with constricted shaft, widely expanded distally with a facet on leading edge; radius notched; occlusal edges of radius and ulna usually enclosing a small foramen; radius and ulna, sometimes also

TABLE 2. Forefin features of *Leptopterygius tenuirostris*.

| Specimen | Humerus wide distally | Humerus with leading edge facet | Foramen between radius and ulna | Radius notched | Phalanges rounded | Fusion between radius and ulna |
|---|---|---|---|---|---|---|
| OUM J10305 | Yes | Yes | Yes | Yes | Yes | Yes |
| BMNH R489 | Yes | Yes | Yes | Yes | Yes | No |
| BGS 51236 | Yes | Yes | Yes | Yes | Yes | No |
| SCM 8372 | Yes | Yes | Yes | Yes | Yes | No |
| WM 527 | Yes | Yes | No | Yes | Yes | Yes |
| GTS L/AG/Arch/18 | Yes | Yes | Yes | Yes | Yes | No |
| BATGM M3552 | Yes | Yes | Yes | Yes | Yes | No |
| BATGM M3556 | Yes | Yes | Yes | Yes | Yes | No |
| BATGM M3565 | Yes | Yes | No | Yes | Yes | No |
| BATGM M3566 | Yes | Yes | No | Yes | Yes | No |
| LEICS OS.90.1953 | Yes | Yes | Yes | Yes | Yes | No |
| DLR '002' | Yes | Indeterminate | Yes | Yes | Yes | No |
| BMNH 36182 | Yes | Yes | Yes | Yes | Yes | Yes |

humerus, may be partially fused; phalanges discoidal, relatively large, probably well spaced distally; femur with slender shaft, expanded distally; tibia notched, probably also tibiale, notches probably broad; pelvic girdle essentially tripartite, though pubis and ischium may be partially fused; coracoid probably rounded and probably always with an anterior notch.

*Geological range*. All specimens here referred to *I. tenuirostris* are from the Lower Lias (and uppermost Triassic; see below), primarily from Street in Somerset but material has also been collected from other localities including Barrow-on-Soar, Leicestershire; Lyme Regis, Dorset; Pinhay Bay, Devon; and Stogursey, Somerset. A pair of partial forefins (BMNH 41253) referable to *I. tenuirostris* were collected from Tewkesbury, Gloucestershire.

Most of the reptilian remains from Street were collected from the Pre-*Planorbis* Beds (Arkell 1933), and while there has been some discussion on whether this horizon should be placed at the base of the Jurassic or at the top of the Triassic, the latter has been recommended (Harland *et al.* 1982). At the other end of the range the youngest material is represented by material from Lyme Regis, and this probably does not extend beyond the earlier part of the Sinemurian. The geological range of *L. tenuirostris* is therefore from the Rhaetian to the Early Sinemurian.

*Description of individual specimens*. See Appendix.

Eurhinosaurus longirostris

Huene's (1922, pp. 39–40) suggestion that *E. longirostris* occurred in England was based on the evidence of two poorly preserved specimens from the Upper Lias of Whitby, Yorkshire (BMNH 14566 and BMNH 36876), which he tentatively assigned to the species. The skull of the first specimen, described as being badly damaged, was said to be exposed from the dorsal aspect, with no mandible visible. The second specimen was described as being a badly damaged skull, again without evidence of a lower jaw.

BMNH 14566 has skull and snout lengths of approximately 860 and 680 mm, and an orbital diameter of approximately 100 mm. If it were assumed that the specimen was not a eurhinosaur and that the mandible was about as long as the skull, the snout and orbital ratios would be approximately 0·79 and 0·12. This snout ratio is consistent with *L. tenuirostris*, despite the fact that the species is not known to extend into the Upper Lias, but the orbital ratio is considerably smaller than that of any other Jurassic ichthyosaur. An orbital diameter of only 100 mm, however, would be consistent with a eurhinosaur skull of 860 mm length. BMNH R5465, for example, the smallest eurhinosaur with comparable data, has a skull length of 1035 mm and an orbital diameter of approximately 125 mm, which gives a value of 0·12 for the orbital ratio, the same as in BMNH 14566. Further preparation or radiography is required for confirmation, but the evidence suggests that BMNH 14566 is referable to *E. longirostris*.

The second specimen, BMNH 36876 (Lydekker 1889, p. 91), is a rather poorly preserved, partially three-dimensional skull, exposed from the left side. The snout, which is in several sections, is long and slender and projects at an angle from the main block. Judged from the narrowness at its terminal end, the snout is

probably almost complete, and has a preserved length of 1025 mm. The orbit is large, almost circular, and contains a fairly well-preserved sclerotic ring. According to Huene (1922, p. 39) there was no lower jaw, but the mandible has been preserved and, although incomplete, its broken tip is only 18 mm deep, indicating that little is missing. The preserved length of the jaw is 600 mm, which is less than half that of the skull (approximately 1280 mm). There can be no doubt of the eurhinosaurian identity of the material, and comparison with BMNH R3938, a similarly sized skull of *E. longirostris* from the Upper Lias of Germany, shows a close correspondence in their measurements (Table 3).

TABLE 3. Comparison of BMNH 36876 with an identified specimen of *Eurhinosaurus longirostris*.

| Specimen | Locality | Skull length | Jaw length | Orbital diameter | Sclerotic diameter |
|---|---|---|---|---|---|
| BMNH 36876 | Whitby, Yorks. | 1280* | 600* | 174 | 70 |
| BMNH R3938 | Probably Holzmaden | 1312 | 648 | 179 | 71 |

* Measurement approximate, with no allowances for missing parts.

A second specimen, also numbered BMNH 36876, is also from the Upper Lias of Whitby. Tentatively referred to *L. tenuirostris* by Lydekker (1889, p. 88), it comprises a partial snout and mandible, exposed from the ventral aspect. The snout and mandibular sections are 850 mm and 600 mm long, giving an overbite of 250 mm. This estimate is based on the assumption that the snout and mandible have retained their natural relationship with one another, but this might not be so. While it is unlikely that the mandible has shifted backwards during preservation, it might have shifted forwards. This is because the mandible could be shifted back from its present position and still retain a close correspondence between its width and that of the snout. There might, therefore, have been a more extensive overbite than the present 250 mm. The material is too incomplete to make a definitive identification, but it is more likely referable to *Eurhinosaurus* than to any other taxon.

*The structure of the tail.* According to Riess (1986, p. 103): '*Eurhinosaurus* . . . did not have a tail-bend. The vertebrae at the end of the tail do decrease in size but there is no sudden decrease of vertebrae in the tail nor a triangular vertebra which would indicate a tail-bend. Furthermore the pictures of unprepared skeletons . . . and sketches of finds which were made available to me by R. Wild . . . all speak one plain language: none of them show even an indication of a tail-bend.' (Translation by E. Wolf.)

Riess illustrated his point by reference to the photographs of FSF 4155 taken before and after preparation (Riess 1986, pl. 1, fig. 2; Hauff and Hauff 1981, pls. 40–41), in which there appears to be no evidence for a natural tail bend. It is certainly true that it has been a common practice during the preparation of Holzmaden ichthyosaurs to remove almost all of the matrix from around segments of the skeleton, such as the tail, and then to drop these into recessed limestone reliefs. The tail bends depicted in such restorations are therefore entirely unfounded, but this does not mean that a tail bend was not originally present, nor that all specimens have been so modified, and each case must be judged on its own merits. Without extensive preparation, the authenticity of an undocumented specimen will always be in doubt, but the identification of wedge-shaped vertebrae in the vicinity of the tail bend is persuasive evidence that a tail bend was present. Given the infrequency with which vertebrae are exposed from the lateral aspect it is not surprising that Riess (1986) should report the absence of wedge-shaped centra in *Eurhinosaurus*. However, I have found a wedge-shaped centrum in the specimen he illustrated (FSF 4155). This vertebra (no. 91) has a diameter of 30 mm and is 15·5 mm wide dorsally and 12 mm wide ventrally. Furthermore, it occurs at a point where there is a marked decline in the rate of reduction of vertebral diameters. It is difficult to deny that a tail bend was present in this specimen, but the angle of the tail bend as depicted in the prepared skeleton may bear little relationship to reality. A careful re-examination of all *Eurhinosaurus* material is obviously needed, but in the meantime it may be noted that this genus probably had a tail bend.

## DISCUSSION

A fairly wide range of variation is seen among the individuals referred to *L. tennirostris*, which raises the question of whether they really do all belong to the same species. How likely is it, for example, that one member of a species has a complex external naris while another has a simple opening, or that one individual has a snout which is considerably longer than that of another? Some measure of the amount of individual variation to be expected within an ichthyosaurian species is obviously required, but there are no criteria for recognizing biological species within the fossil record (except in those rare instances provided by maternal ichthyosaurs—see McGowan 1979). In the absence of direct means of assessing individual variation, *E. longirostris* would appear to serve as a suitable yardstick. This is because, being so highly specialized and distinctly different from all other ichthyosaurs, it is likely to represent a single species, as is its modern analogue, the swordfish (*Xiphias gladius*). It must be remembered, though, that there is great variety in the range of individual variation among living animals, even among closely related ones. *E. longirostris* can, therefore, only give an indication of the degree of individual variation that might be expected within an ichthyosaurian species.

A wide range of variation has been found in *Eurhinosaurus*, both in continuous and discontinuous characters, and some may be attributable to sexual dimorphism (McGowan 1979). Some individuals, for example, have a total digital count of five, others four; the counts to the pelvis and to the tail bend range between 45 and 49 and between 91 and 95; some individuals have a complex bilobed naris while others have a simple opening, and the snout ratio varies between 1·42 and 1·93. The swordfish, similarly, has a wide range of variation in its snout and mandibular proportions (McGowan 1988), and some differences in body proportions are possibly attributable to sexual dimorphism (Alvarado Bremer 1988). The variability seen among specimens here referred to *L. tennirostris*, therefore, probably does represent individual variation rather than the unwitting lumping together of individuals belonging to separate biological species.

The tendency in *L. tennirostris* for the tip of the rostrum to extend beyond the mandible lends support to its possible ancestral relationship to *Excalibosaurus costini*, a species characterized by an extensive overbite (McGowan 1986). The overbite in *E. costini* amounts to about 35% of the snout length, compared with a maximum of about 15% in BMNH 2009, here described as a variant individual of *L. tennirostris* (see Appendix). But the most extreme rostral development is seen in *Eurhinosaurus longirostris*, where the overbite approaches 60% of the snout length. The possibility that *E. longirostris* may have been derived from *Excalibosaurus costini* is discussed elsewhere (McGowan 1986; in press).

The extension of the geographical range of *Eurhinosaurus* into the Whitby locality of England, suggested by Huene (1922), is now established. This is not surprising in view of the similarity in age of the Whitby and Holzmaden localities and of their close proximity (less than 1000 km). Nor is this unprecedented—the predominently German species *Stenopterygius hauffianus*, for example, also occurs in the Upper Lias of Ilminster, Somerset. Wide geographical ranges appear to be the rule rather than the exception for ichthyosaurian species (McGowan 1978).

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## APPENDIX

*Specimens referred to* L. tenuirostris

1. *OUM J10305* (text-figs. 1A and 2A). This almost complete and rather well-preserved skeleton, from Street, comprises a number of blocks set into a plaster relief (McGowan 1974*b*, fig. 12*b*). The matrix lacks chisel marks (see below) and there are no grounds to question the authenticity of the specimen. Because some of the anterior vertebrae are overlain by other bones, difficulties were encountered in making vertebral counts, but the error is not likely to be greater than $\pm 1$. The vertebral column is not sharply downturned, but the presence of a tail bend is confirmed by the presence of wedged-shaped centra at levels 85 and 87 (the feature is obscured in vertebra 86). Thus the centrum of vertebra 85, which is 21 mm high, has dorsal and ventral widths of 8 and 7 mm; measurements for vertebra 87 are 19, 8, and 6 mm, respectively. Because of incomplete preservation, and some displacement of the pelvic girdle, it is not possible to determine the vertebral count to the pelvis with precision; the count is between 45 and 47, and the median value of 46 will be recorded. The pelvic condition is indeterminate.

The tip of the snout has a small (9 mm) extension which may be a displaced tooth, or a bony process from the premaxilla. The former assumption has been made, but if this should prove to be incorrect, 9 mm would have to be added to all relevant measurements. This would elevate the snout, premaxillary, and prenarial ratios from 0.72, 0.52, and 0.60 to 0.74, 0.53, and 0.62, respectively. The external naris has a somewhat bilobed appearance, with an expanded posterior portion. The teeth are slender, especially towards the tip of the rostrum, and are relatively small. One of the larger teeth, for example (at the tip of the maxilla), is 12·5 mm long and 4 mm wide.

There are two partial forefins, the anterior one overlying much of the other and comprising four digits with large discoidal phalanges. The humerus has a relatively narrow shaft, much widened distally, with the leading edge expanded proximodistally forming a facet. This leading edge facet, a distinguishing feature of the species (see Table 2), is also seen in many Upper Lias species (McGowan 1979, pls. 2, 4, 5) and may have served for the transmission of the radial artery and nerve (Johnson 1979, p. 68). The radius has a notch on its leading edge, and the occlusal edges of the radius and ulna enclose a small foramen. An unusual feature of the anteriormost forefin is that the radiale has a small emargination on its distal margin. The otherwise normal appearance of this oblong element discounts the possibility that it has simply been rotated through 90°. The coracoid is largely indeterminate but appears to lack a posterior notch. The hindfin appears to have three digits, the femur is slender shafted and widely expanded distally. The anterior margins of the tibia and tibiale are broadly emarginated.

2. *BMNH R498*. This specimen, from Street, Somerset, comprises several blocks set in plaster, colour-matched to the matrix (McGowan 1974*b*, fig. 12*a*). The matrix bears chisel marks, but the pattern is not like that seen in BGS 51236 or in BMB C2 and, although there are patches of plaster, some with chisel patterns, most of the matrix appears to be original. The tail bend is not an obvious feature because of the dorsal exposure of the skeleton. However, there is evidence of a change in the diameters of the centra at the level of the 85th vertebra, and this probably marks the position of the tail bend. This is confirmed by the presence of wedge-shaped centra; vertebra 84 is slightly wedge-shaped, 85 is markedly so (vertical height of centrum approximately 23 mm, dorsal and ventral widths approximately 7·0 and 4·2 mm), and vertebra 86 is the most strongly wedge-shaped (measurements 20, 9, and 4·5 mm, respectively). The vertebral count to the pelvic girdle is 45. The pelvic condition is indeterminate.

Because the skull, which has been dorsoventrally compressed, lies partially embedded in matrix, few reliable measurements can be made. The external naris is not well preserved but there appears to be an expanded posterior portion, as in OUM J 10305. The teeth are slender.

The forefin, seemingly complete on the right but obviously incomplete on the left side, has a total digital count of four, with 15 elements in the longest digit. The individual phalanges, which are discoidal, are well spaced distally and this appears to be natural rather than manufactured. The humerus has a relatively narrow shaft, much expanded distally, with a well-developed leading-edge facet. The leading edge of the radius is deeply notched. There is no evidence of a foramen between the contact edges of the radius and ulna for the right forefin, but there is evidence of one for the left side. The coracoid is indeterminate. The femur is broadly expanded distally and has a narrow shaft. The tibia and tibiale have broad emarginations on their anterior edges, there are only three digits, and the distal phalanges are discoidal.

3. *BGS 51236* (text-fig. 1B). The initial impression is one of a complete skeleton lying in a single block of matrix that has been worked with a chisel (McGowan 1974*b*, fig. 11). However, some judicious probing with

a mounted needle reveals that the specimen comprises several separate blocks surrounded by an artificial matrix, the whole having been veneered with what appears to be a grey pigmented plaster bearing chisel marks. In places this veneer has cracked, and the original matrix, which has a more yellow colour, can clearly be seen beneath. Many cracks run across the specimen, especially through the post-sacral vertebral column, and some of these are wide and infilled with the grey plaster. It is quite likely that the specimen has been tampered with but this could only be established by an extensive and invasive investigation. The following description, which emends the previous account (McGowan 1974*b*), is therefore given with the reservation that the authenticity of the material is in question.

The vertebral column lacks any obvious tail bend, the tail having been thrown into coils in this region. However, there is evidence of a constriction at level 84 indicating a tail bend, as previously reported, and this now appears to be confirmed by identifying three vertebrae with slightly wedge-shaped centra; the centra of vertebrae 85 and 86 are 21 and 19 mm high, with dorsal and ventral widths of 9 mm and 7 mm and 7 and 6 mm, respectively. The centrum of vertebra 87, which is 18 mm high, is narrower dorsally (7 mm) than ventrally (8 mm) and this would cancel out the downturn effect of the previous centrum. Whether any of the centra anterior to vertebra 84, or posterior to 87, are wedge shaped is not known. In any event it seems unlikely that there was an effective tail bend, which would explain why there is no obvious tail bend in this specimen. The count to the pelvic girdle is 47. The pelvic girdle is tripartite, the pubis and ischium being quite separate.

Close inspection of the skull reveals that the extreme tip of the snout is missing, but it is already so narrow at this point that it is unlikely that very much has been lost, and this is estimated to be about 10 mm. Making allowances for the missing tip changes the previously given cranial ratios; the snout ratio increases from 0·72 to 0·74, the premaxillary ratio from 0·52 to 0·54, and the prenarial ratio increases from 0·60 to 0·61. The mandible, which appears to be complete, stops 9 mm short of the broken tip of the snout, and when allowances are made for the missing tip of the snout this overbite is increased to 19 mm. The orbital ratio has been modified from 0·23 to 0·24. The external naris is bilobed, with a narrow tongue of bone separating a narrow lower portion from the rest. The teeth are very slender; one from the anterior tip of the maxilla is 13 mm long and about 4 mm wide.

Note was taken in the previous account that the forefin measurements were unreliable because the fins had been reconstructed distally. Nevertheless, there is good agreement between left and right sides in the measurements of the humerus, radius and ulna, suggesting that measurements of these elements are reliable. The proximal articular surface of the left radiale looks as if it has been modified to articulate with the radius. The coracoids are rectilinear rather than being typically rounded, raising doubts about their authenticity.

4. *SCM 8372* (text-figs. 1C and 2B). This specimen, which lies on its right side, consists of two main blocks set into a plaster relief, but this has not been made to blend with the matrix and the relationship between the two main blocks, and between their component parts, is good. This is, therefore, considered to be one of the most reliable of the specimens referred to *L. tenuirostris*.

There is a tail bend, which appears to be natural, and vertebra 82, which is at the beginning of the tail bend, is wedge-shaped. The height, dorsal, and ventral widths of this centrum are approximately 19, 9·3, and 6·5 mm, respectively. The centrum of vertebra 84 also appears to be wedge-shaped, but its dorsal and ventral widths are about the same. The apex of the tail bend therefore appears to lie between vertebrae 82 and 84 and the count will be recorded as 83. The vertebral count to the pelvic girdle is 45. The pelvis is tripartite, with no evidence of fusion between the pubis and ischium.

The skull is essentially complete but has been badly crushed, making it difficult to interpret some of its features. There is a particular problem at the tip of the rostrum and it is not clear whether the tips of the right mandible and right side of the snout are being seen, or whether the mandible stops short and what is being seen are the tips of the left and right halves of the snout. The assumption is made that the mandible extends to the tip of the snout. A sub-terminal portion of the rostrum—a segment about 140 mm long—was stolen from the specimen while on display, and has been restored in plaster. Teeth are not plentiful, though several can be seen, and these are small and very slender. A tooth from close to the tip of the snout, for example, is 9 mm long and about 1 mm wide. The external naris appears to be bilobed, but further preparation is needed to determine its shape. The naris appears to be continued anteriorly as a narrow slit, reminiscent of the condition in *Excalibosaurus costini* (McGowan, 1986) but this could be an effect of preservation. This crack-like extension is separated from the external naris proper by a constriction, and the latter has been taken as the anterior boundary of the naris in all measurements. If the anterior extension is later determined to be an integral part of the naris, it will be necessary to decrease the prenarial ratio from the present value of 0·61 to 0·59.

The forefin, which has only 10 elements in the longest digit and is probably not complete, has three or perhaps four primary digits and a total digital count of four, possibly five. The humerus has a narrow shaft, is broadly expanded distally, and has a prominent leading edge facet. The anterior edge of the radius is broadly notched and a prominent foramen is enclosed between the contact edges of the radius and ulna. The coracoid is rounded, not angular as in BGS 51236, with a fairly broad anterior notch. The posterolateral margin appears to be scalloped but this has probably been caused by its being crushed against the underlying ribs.

5. *WM 527*. This specimen, from Mandeville, near Street, is preserved from the dorsal aspect and faces towards the left. It would appear to lie on a single slab of matrix, but this is much cracked and infilled and, without an extensive investigation, it cannot be determined whether all the parts belong together. However, with the possible exception of a crack immediately posterior to the pelvic girdle, there is nothing to arouse suspicion and the assumption is made that the specimen is authentic. Although the entire length of the skull is preserved, the skull roof has been lost so that few measurements can be taken. Furthermore, although the posterior limit of the mandible can be determined, its anterior tip cannot. The assumption is made that the mandible extended to the tip of the snout because this is the usual situation. The vertebral count to the pelvic girdle is approximately 45. The pelvis is fairly well preserved and clearly shows that the pubis and ischium are not fused.

The most complete of the two forefins is well preserved but is incomplete distally. The humerus has a narrow shaft, is much widened distally, and has a prominent leading edge facet. The radius and radiale are notched but there is no foramen between the radius and ulna. The radius is partially fused with the humerus and with the ulna. The coracoid is largely indeterminate, being overlain by other elements, but it appears to be rounded, not rectilinear as in BGS 51236.

6. *GTS L/AG/Arch/18*. This near-complete skeleton from Street lies on its right side, and comprises two major blocks, set in plaster. Some of the matrix bears chisel marks, but these appear to be genuine. The vertebral column has a distinct tail bend, but an oblique crack across the matrix at this level has been infilled with plaster, painted to match the colour of the matrix. This raises the possibility that the specimen has been tampered with but it is most unlikely that the bend has been manufactured from an originally straight tail because this would have required inserting a wedge of matrix, which has not been done. The possibility cannot be dismissed that the segment posterior to the crack has been added from a second specimen, though the two broken edges, which are only separated by a gap of about 3 mm, appear to correspond with one another fairly well. For the present it will be assumed that the vertebral column is complete. The vertebral counts are difficult to make because of displacements in the thoracic region, and could be underestimated by between two and three; the counts to the pelvis and to the tail bend are 44 and 86. The centrum of vertebra 86, which is approximately 20 mm high, is slightly wedge-shaped, being 9 mm wide dorsally and 7·5 mm ventrally. The pubis and ischium are unfused.

An unusual feature of this specimen is that most of the rostral portion of the skull is missing, as are the anterior portions of both mandibles. Indeed, all that remains of the mandibles are the surangulars, and while this preservation is unusual it is not without precedent because there are two isolated surangulars in the collections of the British Museum (BMNH 2122X and 2129X). No measurements are possible for the skull.

The forefins are typical of *L. tenuirostris*. The humerus has a narrow shaft, widely expanded distally, with a leading edge facet. The radius is deeply notched and encloses a prominent foramen with the ulna. There are four digits, the phalanges are discoidal and there are only 11 elements in the longest digit of the most complete (right) fin, though there are probably a few elements missing terminally. Neither the coracoids, nor the hindfins, are well preserved.

7. *BATGM M3552*. This skeleton, which lies on its right side, comprises a skull—complete except for its tip—a fairly complete and well-preserved forefin and coracoid, and scattered vertebrae and ribs. The blocks bearing the bones are set in plaster but the relationships between them appears to be good. No vertebral counts are possible.

The tip of the snout and mandible have been partially and inexpertly restored in plaster and it is estimated that approximately 20 mm has been lost. This has been taken into account in the cranial measurements, which are therefore partly estimated. The snout is long and slender, typical of the species. Teeth are numerous, slender, and are about 1 cm long. The orbit is well rounded; the shape of the external naris is indeterminate.

The humerus is fairly broad distally, and has a leading edge facet. The radius and radiale are both notched, and a prominent foramen is enclosed between the radius and ulna. The phalanges are discoidal, but the fin

is too incomplete to determine either the number of elements in the longest digit, or the number of digits—three digits are preserved. The coracoid is rounded, with a broad anterior, and a posterior emargination.

8. *BATGM M3556*. This partial skeleton from Street appears to be exemplary of the species but, because of its generally poor preservation, few measurements can be taken. The skeleton lies on its left side, but the left forefin has been flipped up above the vertebral column, where it rests on its ventral surface. The block bearing the skeleton is set in a plaster relief and has numerous cracks running through it, some deep and wide. Little remains of the postsacral skeleton; the vertebral count to the pelvis is 46, possibly 45. The pelvic girdle is well preserved and there is partial fusion between the pubis and ischium.

Most of the prenarial segment of the skull is missing, and that which remains is incomplete and displaced. The few scattered teeth that can be seen are relatively small, and while some are very slender others are conical.

The forefin has four digits, the phalanges are discoidal, the radius is notched and there is a foramen enclosed between the radius and ulna. The humerus is broadly expanded distally and has a well-developed leading edge facet. The coracoid is longer than it is wide, tends to be rounded rather than rectilinear, and has a single, round, anterior notch that is relatively small. Little remains of the hindfin; the femur is fairly slender and widens distally, as in other referred specimens. The tibia has a broad notch that occupies much of its leading edge.

9. *BATGM M3565*. This partial skeleton, which lies on its left side, comprises several blocks set in plaster. The skull has several cracks and repairs, and while the contact edges of the broken elements appear to match satisfactorily, it is not known how good these matches are. The accuracy of the cranial measurements are therefore uncertain. No vertebral counts could be made; the pelvic girdle is indeterminate.

The snout and mandible are both long and slender, typical of the species, but the orbit appears rather large. The orbital ratio is correspondingly high (0·24) but is within the limits previously diagnosed for *L. tenuirostris*. The external naris, which also appears to be relatively large, has something of a posterior expansion, but its shape is partially obscured by a displaced bone. Teeth occur throughout; they are slender and relatively small and one of the largest ones is 11 mm long and 4 mm wide.

The forefin is robust. The humerus is broad, widely expanded distally, and has a prominent leading edge facet. There appear to be four digits and the phalanges are discoidal. The radius and radiale are both notched, but there is no foramen enclosed between the radius and ulna. The coracoid is longer than broad, with a relatively long and straight intercoracoid facet and a single anterior emargination.

10. *BATGM M3566*. This large and incomplete skeleton lies with the skull, which lacks jaws, exposed from the ventral aspect. The specimen essentially occupies a single block set in plaster. No vertebral counts can be made and there is no determinate pelvis.

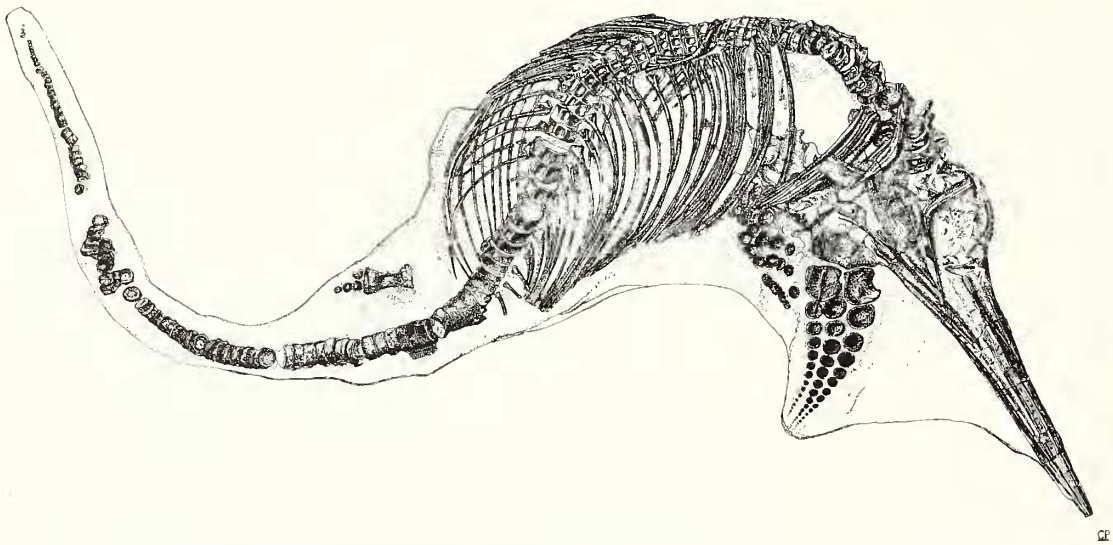
The skull is approximately 690 mm long and is the second largest referred specimen treated here. The snout is long and slender but few measurements can be taken because of its orientation. Few teeth are preserved and these are relatively small and are conical rather than slender. One of the largest teeth is 9·6 mm long and 4 mm wide.

The humerus has a constricted shaft and is widened distally, typical of *L. tenuirostris*, but it has a relatively small leading edge facet. The radius is notched but there is no foramen enclosed with the ulna—the remainder of the fin is indeterminate. The coracoid is considerably longer than it is wide (length 125 mm, width 75 mm) with a discrete anterior notch; the posterior edge appears to be broadly emarginated. The well-preserved scapula is robust.

11. *LEICS OS.90.1953*. The snout of this rather poorly preserved skeleton, from Barrow-on-Soar, Leicestershire, is incomplete, and it is not possible to estimate how much has been lost. Conceivably the snout could have been extremely long, as in BMNH 36182 from the same locality, and the specimen might therefore be atypical of the species (see p. 425 below). Few measurements can be taken from the skull, or from the rest of the skeleton, but the material is considered important enough to be included here, especially since it is only one of three specimens from this locality. The skeleton is exposed from the right side and comprises several blocks that have been set into a plaster relief. The vertebral column is depicted as being straight but the caudal vertebrae, which have been largely freed from matrix, have been arranged in a line without any obvious keying-up of the individual segments. Therefore, if a tail bend had been present when the specimen was found, this would have been lost during preparation. A disturbance in the regular order of the vertebrae occurs at about level 85 which may mark the position of a tail bend, but wedge-shaped centra cannot be seen. The vertebral count to the pelvic girdle is 48.

The external naris requires some preparation, and although it appears to have a simple petaloid shape there is indication of a slit-like extension of its anterior boundary. Poor preparation obscures most of the details of the teeth, but they are numerous and appear to be slender.

The incomplete forefin has a humerus with a relatively narrow shaft, much widened distally and with a leading edge facet. The radius bears a prominent notch on its leading edge and a small foramen is enclosed between the contact edges of the radius and ulna. The slender femur has a wide distal expansion.



TEXT-FIG. 3. DLR '002', probably representing a mature individual of *L. tenuirostris*, ×0·06. Drawing by C. M. Pamplin, who kindly gave permission for its inclusion here.

12. *DLR '002'* (text-fig. 3). This rather important skeleton is tentatively identified as being a mature individual of *L. tenuirostris*. It was found in 1979 by Robert Langham in Pinhay Bay, just west of Lyme Regis, in the adjoining county of Devon. The horizon is given as that of *Arietites bucklandi*, which places the material at the beginning of the Sinemurian. The skeleton, which is almost complete, lies with its left side embedded in a thin sheet of matrix which has been trimmed to the approximate outline of the skeleton. Its arched posture has given rise to the epithet, 'the leaping ichthyosaur' (Pamplin 1987). The material has undergone considerable compression; the skull, for example, is only about 13 mm thick at the level of the external nares. This has undoubtedly distorted the specimen, exaggerating the depth of the skull and mandible and making the humerus appear much broader than it was in life. The tip of the skull broke off during collection, an estimated loss of approximately 10 mm (Robert Langham, pers. comm.) having been allowed for in all relevant measurements. The single hindfin, which is incomplete, was placed in its present position during preparation and is therefore not in its natural position.

There is no obvious tail bend but there is a disturbance in the orderly arrangement of the vertebrae at about level 83, and this is accompanied by a marked decrease in the diameters of the centra. Close inspection reveals that vertebra 85 is wedge-shaped; the centrum has a height of 31 mm and is 14 mm wide dorsally and 11 mm wide some two-thirds of the way down (the ventral width, which is less than 11 mm, cannot be measured without further preparation). The pelvic girdle has not been preserved and since the hindfin is not in its natural position it cannot be used to determine the level of the pelvis. However, given that ichthyosaurian ribs become reduced in length at the level of the pelvic girdle, it is possible to estimate the position of the pelvis by detecting this change. The rib associated with vertebra 46 is 70 mm long while those of vertebrae 47 and 48 are both 53 mm long. This indicates a vertebral count to the pelvis of approximately 47.

The skull has a long slender snout and the snout ratio of 0·75 falls within the diagnosed limits for *L. tenuirostris*. The orbit is difficult to measure because of uncertainties in its posterior margin, but an estimate of its diameter gives an orbital ratio of 0·18. While this is lower than that of specimens that

have been referred, without reservation, to *L. tenuirostris*, it is comparable to that of one tentatively referred specimen (BMNH 36182—orbital ratios 0·16). Because of poor preservation the anterior tip of the maxilla is difficult to discern, but an estimate of its position gives a value of 0·53 for the premaxillary ratio, which is within diagnosed limits for *L. tenuirostris*. The same holds true for the prenarial ratio of 0·58. The external naris is not immediately apparent because of the effects of crushing, which has caused the elements forming its borders to be flattened against the bones of the other side of the skull. The naris is remarkable for its large size and for its complex bilobed shape. Anteriorly it is continued as a narrow slit, as in SCM 8372, but whether this is truly part of the naris or merely a result of crushing cannot be determined. The teeth are far more sparse than they are in most other specimens (e.g. OUM 10305, BGS 51236, and LEICS OS.90.1953) and are relatively minute compared to the size of the skull; one of the largest teeth is only 13 mm long and 3 mm wide.

The best preserved forefin appears to be complete, but has been restored in plaster distal to the first row of phalanges (Peter Langham, pers. comm.). It is, therefore, not possible to determine the total number of elements in the longest digit, and the total number of digits may have exceeded the three that have been preserved. The humerus appears to be rather broad, but this is almost certainly attributable to crushing and the shaft is obviously narrow, typical of *L. tenuirostris*. It is not possible to determine whether there is a leading edge facet because this region is partially overlain by the displaced left mandible. The radius is notched, and a foramen is enclosed between the radius and ulna. Both coracoids are fairly well exposed and are rounded, almost discoidal in shape, with a small notch on the anterior margin.

Referring DLR '002' to *L. tenuirostris* extends the upper size limit of the species considerably, but it is fairly certain that it is correctly assigned because its other features are typical of the species, namely: relatively long snout, complex external naris, vertebral count to the tail bend of approximately 85, distally expanded humerus, notched radius, foramen enclosed between the radius and ulna.

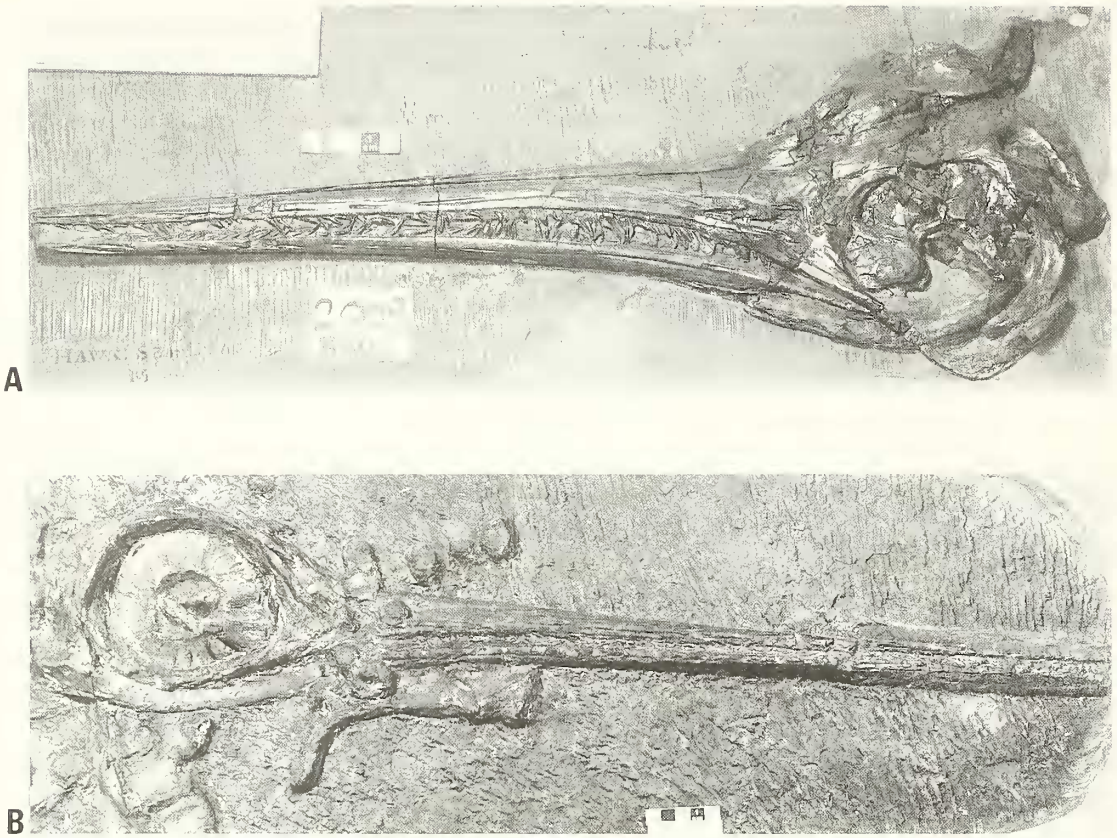
*Atypical specimens probably representing variant individuals of* L. tenuirostris

1. *BMNH 2009* (text-fig. 4A). This well-preserved skull, which is exposed from the left side, was figured by Hawkins (1834, pl. 13). Initially the skull appears to be a perfectly ordinary example of *I. tenuirostris*, but closer inspection reveals two departures from the norm, namely an extensive overbite and an unusually slender mandible. Before these features can be discussed it is necessary to consider the state of preservation.

The tip of the snout appears to lie at the same level as that of the mandible, but this is not so because the two halves of the mandible have moved relative to one another and what appears to be the tip of the left mandible, lying in line with the tip of the left side of the snout, is in fact the *right* half of the mandible. The tip of the left half of the mandible lies about 18 mm posterior to the tip of the snout, giving an overbite of the same amount. But the overbite is in fact greater than this, for two reasons. First, the very tip of the snout is missing—between 10 and 20 mm. Secondly, the left mandible has been displaced forwards, the posterior end of the left mandible having come to rest about 20 mm anterior to the posterior margin of the orbit. To restore the left mandible to its natural position would require moving it back about 30 mm. Allowing for this, and for the missing tip of the snout, gives an overbite of between some 60 and 70 mm, which is about 15% of the length of the snout. Having an elongated snout and an abbreviated jaw gives the relatively high value of 0·89 for the snout ratio.

Remarkable too is the relative slenderness of the jaw. This is revealed by comparing BMNH 2009 with OUM J10305, a typical specimen of *L. tenuirostris* of similar skull length (Table 4). Although their snouts are similar in depth, the jaw is only about half as deep in BMNH 2009, and the snout is longer and the jaw shorter. In other characters, including the possession of slender teeth and a relatively long external naris (its outline is partly obscured by a displaced tooth), BMNH 2009 is typical of *L. tenuirostris*. I conclude that the specimen probably represents a variant individual, and the data will not be used to contribute to the diagnosis of the species.

2. *BMNH 36182* (text-fig. 4B). Owen's 'least incomplete' exemplar of *I. longirostris* (1881, pp. 124–126, pl. 32, fig. 7), is a large, almost complete skeleton which lies with its right side exposed. The material is quite well preserved, but its preparation could be much improved by further work. The bone and matrix are a distinctive dark brown, which appears to be characteristic of its Barrow-on-Soar locality, and the matrix is very hard. Several deep cracks run through the specimen, and there is a large gap in the vertebral column at the level of the pelvic girdle which has been filled in with a cement. However, the specimen has probably not been tampered with. The most striking feature is the remarkably long and slender snout, unsurpassed in any of the material hitherto referred to *L. tenuirostris*. There are no comparably sized skulls of *L. tenuirostris* with adequate data for comparison, but in BGS 51236, which is less than two-thirds as long, the depths of




TEXT-FIG. 4. Specimens probably representing variant individuals of *L. tenuirostris*. A, BMNH 2009, ×0·26. B, BMNH 36182, ×0·19.

TABLE 4. Comparison of BMNH 2009 and OUM J10305.

| Specimen | Skull length | Jaw length | Orbital diameter | Snout length |
|---|---|---|---|---|
| BMNH 2009 | 539·0* | 482·0 | 100·0 | 429·0* |
| OUM J10305 | 523·0 | 550·0 | 114·0 | 398·0 |
| | | SNOUT DEPTH | | |
| | S-S2 | S-J2 | S-M | S-N |
| BMNH 2009 | 14·6 | 15·3 | 20·5 | 32·0 |
| OUM J10305 | 14·0 | 20·0 | 20·0 | 33·0 |
| | | JAW DEPTH | | |
| | J-S2 | J-J2 | J-M | J-N |
| BMNH 2009 | 11·0 | 8·5 | 10·0 | 14·6 |
| OUM J10305 | 16·0 | 21·0 | 22·0 | 25·0 |

* Allowance made for missing tip of snout.

TABLE 5. Comparison of BGS 51236 and BMNH 36182.

| | SKULL LENGTH | SNOUT DEPTH | | | |
|---|---|---|---|---|---|
| Specimen | | S-S2 | S-J2 | S-M | S-N |
| BGS 51236 | 570·0* | 21·5 | 26·3 | 28·0 | 40·8 |
| BMNH 36182 | 760.0* | 14·0 | 18·0 | 25·0 | 36·0 |
| | | JAW DEPTH | | | |
| | | J-S2 | J-J2 | J-M | J-N |
| BGS 51236 | | 17·2 | 18·0 | 19·0 | 26·0 |
| BMNH 36182 | | 10·0 | 12·0 | 14·0 | 16·0 |

* Allowance made for missing tip of snout.

the snout and jaw all exceed those of BMNH 36182 (Table 5). The snout appears to be relatively long, but the snout ratio (0·78) is the same as that of BMNH R498. Although the orbit appears to be prominent (Owen 1881, p. 125 commented that it was relatively larger than in *L. tenuirostris*) it is relatively smaller (orbital ratio 0·16) than in any referred specimens of *L. tenuirostris*. Few teeth can be seen, and then only their tips, and it is not clear whether this is due to poor preservation, poor preparation, or to tooth reduction. The external naris is largely obscured by overlying bone, but it appears to have the shape of a curved ellipse.

There is no tail bend and it is not possible to discern any wedge-shaped centra. However, there is a disturbance in the orderly arrangement of the centra between vertebrae 80 and 84, accompanied by a marked decrease in their diameters, and this might indicate the position of a tail bend. The vertebral count to the pelvis is probably 45 (Owen counted 48). The pelvic girdle is partly indeterminate, but the pubis and ischium are certainly not fused proximally.

The best preserved forefin is incomplete and the humerus is partially fused with the radius which makes it difficult to determine its shape. The humerus appears to be expanded distally, there are four digits, and the phalanges appear to be discoidal. There is a well-developed foramen between the radius and ulna in one fin (the least complete fin), with some indication of one in the other, and the radius is deeply notched. In all of these features the material is typical of *L. tenuirostris*. The coracoid is indeterminate.

The unusually slender rostrum no doubt influenced Owen's (1881) decision to refer this specimen to a separate species from *L. tenuirostris*. However, aside from this feature, and the relatively small orbit, the material is consistent with what is known of *L. tenuirostris*, and it is concluded that it probably represents a variant individual of the species. Further preparation might help clarify the situation, but for the present the material is tentatively referred to *L. tenuirostris*, though its data were not used to contribute to the diagnosis of the species.